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NR. 1. POUL HEEGAARD: LARVAL STAGES OF *MEGANYCTIPHANES* (*EUPHAUSIACEA*) AND SOME GENERAL PHYLOGENETIC REMARKS

KØBENHAVN
C. A. REITZELS FORLAG
BIANCO LUNOS BOGTRYKKERI
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LARVAL STAGES OF *MEGANYCTIPHANES (EUPHAUSIACEA)* AND SOME GENERAL PHYLOGENETIC REMARKS

BY

POUL HEEGAARD

WITH ONE TEXTFIGURE AND FOUR PLATES

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Introduction.

On account of the great irregularities in the development of the larval forms of the Euphausiacea, which do not pass through any "fixed stages", it has been, and is still, very difficult to obtain a full knowledge of the larval development of this group. It also appears that owing to the great resemblance between the larvae of the different species, especially in their younger stages, there is a possibility of confusing the respective larvae in the literature. These facts became clear to me when I studied the larval development of *Meganyctiphanes norvegica* at the Kristineberg Zoological Station, Gullmarfjord, in the spring of 1947. In this locality only one species of Euphausiacea occurs, viz. the above mentioned species, and moreover, as the larvae of this species in the Gullmar Fjord are only found behind a barrier in 60 m. depth far from the remaining area of distribution of the Euphausiacea, there is no possibility for mistake as regards the identity of the Euphausiacea larvae collected here.

Although the investigation has not yet been definitely completed so many new facts have already been gained that I think it justifiable to publish the present paper.

Historical survey.

The first description of the larvae of the Euphausiacea was given by DANA (1852), but he was not aware that the animals he described were the larvae of the Euphausiacea. This was shown by CLAUS (1863), who also described some larval stages from the Mediterranean. — These descriptions were later somewhat further elaborated by METSCHNIKOFF (1869, 1871). The first fairly large work on the Euphausiacea larvae, however, was the treatise on the "Challenger" material by SARS (1885), and in 1898 he described the youngest stages of *Meganyctiphanes norvegica*. Of later authors, mention should be made of LEBOUR (1924, 25, 26, 27), who described the development of some northern species.

Common to all these (except SARS') works is the view that the development stages are fixed, and that each variation in the larval forms must represent a separate stage. The result is that a very considerable number of stages have been described. Thus in the case of *Nyctiphanes couchii* (BELL) LEBOUR found no less than 31 larval stages. She concluded, however (1925, p. 525), that "there is a distinct evidence of the jumping of stages in some species" and that "Distinctive stages nearly always seems to occur as though certain stages were dominant."

In 1908 HANSEN called attention to the fact that in three of the Antarctic species investigated by him the development does not follow parallel lines. On the contrary, the succession of the development of the different organs appears to vary from one species to the other. This point of view is further elucidated in his papers of 1910 and 1912.

Lebour's investigations especially, in connection with his own researches, induced Macdonald (1926) to suppose "that the act of ecdysis does not by any means form a fixed landmark in the developmental history of the individuals." In his main work (1927), however, he abandons this theory, maintaining instead that certain of the stages are dominant, from which he concluded (p. 792) "that it would appear that during the development of *Meganyctiphanes norvegica* in the Clyde Sea Area the furcilia period is one of instability, and that we have here evidence of an incipient shortening of the larval existence by the numerical reduction of instars in addition to a hastening of development by the earlier appearance of the luminescent organs and growth of the thoracic appendages." Rustad (1934) likewise emphasizes the dominance of certain stages and draws the following conclusion (p. 69): "Considering now the single species we can state that the earlier part of the development is almost schematic, with no room for individual variations of importance, whereas in the late stages the specimens may show great variations, which may even in greater or less degree efface the schematic picture of the development."

These thoughts were definitely put in form by Fraser (1936). He proved, what had been suggested by Macdonald and Rustad, that there was not only a variation in the development between the different species but that there also existed an individual variation within one and the same species. The organs which had specially been dealt with as regards relative variation during the development were the pleopods. Fraser further comes to the conclusion (p. 35) "that each pleopod appears at first in the non-setose form and is provided with setae at the next ensuing moult." By following the law of development thus set forth, and at the same time by recognizing the individual variation of appearance of the pleopods he assumes that the species investigated by him, *Euphausia superba*, has only 12 larval stages, plus some odd "adolescent" stages. Later investigators, e. g. John (1936), Frost (1939), and Einarsson (1945) have followed Fraser as regards this point of view.

Frost, who in 1935 assumed that the neritic forms had more larval stages than the oceanic, in 1939 explains this according to Fraser's theory of development as follows: "there does seem to be a difference in the number of variants of the Furcilia found in neritic and oceanic species. — In general the "oceanic" species appears to have stabilized their Furcilia development more than the "neritic" species have done." He suppose that relatively higher temperatures and salinities have a stabilizing effect on the stages, while the instability of the neritic forms is due to a low salinity and a low temperature. We shall later see that if this difference between oceanic and neritic holds true, it must be supposed to be due to other conditions than a higher or lower salinity and temperature. Finally Einarsson (1945) seems to be of the opinion that it is only the pleopods that are variable in the different stages, for he gives a fixed description of the other appendages for each single stage.

Larval development.

In the spring of 1947 the first eggs began to appear in the Gullmarfjord about the 25th of April, the ice not having left the fjord until the beginning of April. About the 1st of May the eggs were found in large numbers in the plankton, especially in the lowermost 10—15 metres of the deeper part of the fjord, where the adult animals also occurred in rather dense masses. At this time the temperature of the water was c. 4° Centigrade. The temperature rose, however, somewhat during the summer. At the beginning of May the first Nauplii began to appear,

increasing considerably in number during the first half of that month. Without being able to state anything definite, I have the impression that the development of the eggs from the time of spawning to the time of hatching takes about five to six days. The ensuing Nauplius stages are fairly short, the Nauplius and the Metanauplius stage each lasting about 3—4 days, and almost the same appears to be the rule for the following Calytopis stages, the duration of which are perhaps a little longer; finally, the Furcilia stages appear to last from 7 to 8 days each, the first stages a little less, the later stages somewhat longer. However, not having had the opportunity of following the development beyond the fourth Furcilia stage, I am unable to give any information about the duration of the later developmental stages.

The development itself has been thoroughly described by SARS (1898), LEBOUR (1924, 1925), and others, so I shall refrain from going into more detail here, and shall merely discuss a few points.

LEBOUR (1924, p. 413) sets forth the supposition that the *Meganyctiphanes* perhaps carry their eggs for a short time, like so many other Euphausiacea, but admits, however, that the finding of free, unicellular eggs by SARS, speaks against such a supposition; nor has it ever been observed. To this I may add that I have investigated numerous adult specimens both before and after spawning, and in my plankton hauls I have collected several thousands of eggs, practically all of which were at first found to be newly spawned and unicellular, but I have never observed anything which might indicate that the *Meganyctiphanes* carry their eggs on them.

Larval stages.

The first larval stages have never given rise to any doubt. SARS (1898) describes two Nauplius stages, one Metanauplius stage, and three Calytopis stages. But here the agreement ceases. The larva now passes into the stages designated as the Furcilia stages, the number and appearances of which have been given much trouble and difference of opinion. As mentioned in the historical introduction, this began with LEBOUR's description of the larval stages of *Meganyctiphanes* (1924, 1925) in which every larva differing in any way from the earlier ones was considered as a new stage. But LEBOUR herself realized that she was somewhat wrong in this. All these numerous "stages" could not reasonably be assumed to form a continuous succession within the present material of larvae, just as the duration of the development would hardly agree with the immense number of stages (more than thirty). LEBOUR, trying to find an explanation of this, says (1926, p. 525) that in a genus "distinctive stages nearly always seem to occur as though certain stages were dominant." This applies only to the Furcilia stages, the three Calytopis stages of SARS having thus been accepted without further discussion; but SARS himself says about the Calytopis stages (1898, p. 27]: "In the following pages three different stages will be described, but there are several intermediate stages connecting those here described." Thus, in the Furcilia stages the same variation within one and the same stage was not accepted, which had been accepted without objection for the Calytopis stages by reducing them to three stages. Perhaps this difference in opinion may be due to the fact that SARS' statement regarding the variation has been overlooked, and that the material of Calytopis stages has been too small to enable the later authors to ascertain this variation. As mentioned in the historical survey RUSTAD (1934) even goes so far to consider the earlier developmental stages as "almost schematic", and states (p. 69) "that the younger stages, including the Calytopis stages, present a marked uniformity."

Macdonald (1926, 27, 28) also is aware that something is wrong, and he tries to explain this as due to local shortenings of the development in the Clyde Area, where his investigations were made. Not till 1936 did Fraser succeed in putting forward a more probable explanation.

What had especially been emphasized as regards these different larval stages was the variation of the pleopods in the Furcilia stages, these being the easiest observable parts of the animal. Even at a low magnification, and on poorly preserved material, it was easy to observe the number of the pleopods on the abdomen and whether they were setose or non-setose. Most authors appear to have been satisfied with this although as early as 1898 Sars had called attention to the existence of "several intermediate stages", by which he indirectly expressed that the variation concerned all the organs and parts of organs, all these parts varying in the three stages described by him. Einarsson (1945), in his desire to state the greater stability in the stages for oceanic than for neritic forms, perhaps minimized the variation a little, excepting, of course, the pleopods.

If the development is followed in one locality and a sufficiently large series is secured, it will be found to be relatively easy to distinguish the individual stages, and, as already mentioned, it will be found that each stage lasts for about 8 days, which facts at first may also be helpful in the distinction of the stages. During my stay at Kristineberg I had the opportunity of following the development to and including the fourth Furcilia stage. At the same time I made some measurements of the larvae. Altogether 98 larvae were measured of which the 86 were Furcilia larvae. The average lengths of these larvae, measured from the rostrum to the distal-most point of the telson (setae, however, not included) were as follows:

Calytopis I	0,85 mm
Calytopis II	1,57 mm
Calytopis III	2,13 mm
Furcilia I	2,69 mm
Furcilia II	3,26 mm
Furcilia III	4,16 mm
Furcilia IV	5,42 mm

On comparing these measurements with those given by Einarsson (1945, pp. 22—24) it will be seen that the three Calytopis stages show fairly good agreement, but regarding the furcilia stages it would seem that, Einarsson is one stage behind, his first Furcilia stage corresponding to my second Furcilia stage, and so on. If we then look at his formula for the development of the pleopods (p. 9) we shall find that in Einarsson's larvae all the pleopods are fully developed already in the third Furcilia stage. A closer study of Einarsson's scheme for the development of the pleopods in the *Meganyctiphanes* reveals that in this scheme he has omitted 2 setose — 2 non-setose pleopods, which were present in the material investigated by him, as mentioned by himself. If this pleopod-formula is included, we would get four Furcilia stages, not three, before we reach the five setose pleopods; but as this formula was dominant in the material from a few stations only he (p. 23) left it out of consideration.

There is, however, another point in Einarsson's scheme, viz. that for this species he has no Furcilia larva completely without pleopods. This fact is all the more interesting since all the other investigators have described this form, thus Lebour (1925) from Plymouth, and Macdonald (1927) from the Clyde Sea Area. Personally I have now found the same stage in the Gullmarfjord (Fig. 16). It should be added that during the first eight days of the occurrence of Furcilias in the Gullmarfjord none of the larvae caught in the plankton net had pleopods.

This, as well as the measurements and the development of the other appendages in the non-pleopod larvae, indicates that these larvae represent a first Furcilia stage, and, as three different investigators have found the larvae in three widely different localities, that it will be necessary to take this stage into account also; thus, if the following larval stage does not get all the five pleopods at one time — which it does not, as shown by the statistics — then the earliest stage, which may have five setose pleopods, must be the fourth Furcilia stage.

The last question in this connection is then: does the oceanic specimens of the *Meganyctiphanes* develop without this stage at Iceland, whence EINARSSON obtained his material, contrary to the development in the three other investigated localities with neritic specimens? This cannot be answered with certainty but it would be against EINARSSON's own opinion that, not the number of stages but only the variation of the stages is different in oceanic and neritic forms. If EINARSSON is right in this opinion, he has overlooked a larval stage in *Meganyctiphanes*. It should, however, be borne in mind that EINARSSON's material consists of preserved material collected on expeditions, which, of course, can never give such a sure and general representation as may be obtained by collecting one and the same species in one and the same locality over a certain period of time, as was done by the three investigators of neritic forms. Furthermore this non-pleopod larval stage is found in most other Euphausiacea species.

In order to show that the individual variation within one and the same larval stage is not limited to the pleopods alone, I have, as an example, studied the pereiopods in some specimens representing the first four Furcilia stages. The pereiopods were divided into nine groups according to their degree of development. In order to give the reader an impression of how these degrees of development differ from each other I have figured some of them on the plates. Thus degree I is shown in Fig. 16, degree II in Fig. 34, degree III in Fig. 35, degree V in Fig. 36, degree VII in Fig. 37, and degree IX in Fig. 38. The 82 Furcilia-larvae investigated were distributed in the following way:

Developmental degree for pereiopods	I	II	III	IV	V	VI	VII	VIII	IX	Number of larva
Furcilia I	2	3	2	..	..	..	..	..	..	7
Furcilia II	..	1	3	1	4	1	..	..	..	10
Furcilia III	..	..	..	..	15	18	19	1	..	53
Furcilia IV	..	..	..	..	..	..	2	3	7	12
										82 larvae

We find here a quite natural continuous development which may almost be said to be interrupted artificially by the ecdyses necessary for the growth. It must be regarded as a primitive character that the ecdyses have not yet exerted a dominant influence on the entire development. Theoretically we might just as well, instead of chosing the pereiopod or, as formerly, the pleopods, have chosen the development of any other organ, e. g. the mouth appendages, the eyes, the luminescent organs, etc. But here the variability will by the nature of the case be less, and accordingly less striking.

The Euphausiacea larvae must be considered as rather primitive Malacostraca, which is also indicated in several other ways. In these primitive forms the shape of the larval stages, and perhaps also their number, has not yet been fully genetically fixed. A more or less continuous development takes place inside the shield, but outwards this is somewhat obscured,

the exoskeleton not allowing any exterior changes except in connection with the ecdyses. These ecdyses appear to occur with more fixed intervals than the growth, which apparently goes on continuously beneath the shield. We therefore find that not all the larvae have reached the same degree of development inside their old cuticle when the next ecdysis takes place. The new shape of the cuticle is of course determined by the surface of the animal when the old cuticle has been shed, and we therefore get the above-mentioned individual variation, which is found to exist between the larvae, in spite of the fact that the respective larvae have all passed through the same number of ecdyses.

Actually there is nothing peculiar about these points of view, though they may perhaps seem so for a moment. Something similar is known to occur in the insects, in the Orthoptera, where we speak of an incomplete development which precisely means a gradual growth from larva to adult, as far as the exoskeleton permits. The thin cuticle of the larva has a limited life-time, and, on the other hand, the growth takes place uniformly being subject to rather great individual variations, the result being that the stages cannot be fixed, but must show a rather considerable individual variation. This variation appears to be less pronounced in the oceanic than in the neritic species. Rustad (1934) attempts to explain this by supposing that the temperature and the salinity of the water are higher where the oceanic forms live than where the neritic forms live. That this difference generally exists as far as the salinity is concerned cannot be denied, but it certainly does not hold good for the temperature. We find oceanic forms in the Arctic and the Antarctic which live under much lower temperature conditions than do most of the neritic forms. But hardly any of these factors exerts a dominant influence on the growth, their variations must generally be supposed to be so small that they do not inhibit the development of the larvae. On the other hand, other factors may be pointed out which are different near the shore and out in the open sea. In the open sea all conditions are either good or bad for the larvae. They are more constant, so all the larvae get almost the same food- and growth-conditions at the same time. That even the oceanic larvae show certain individual variations, corresponds to the fact that the pups of the same litter do not grow at completely the same rate even though they live together and get the same care. If the care and the food of the individual pups is varied, then, of course, the variation in their growth becomes considerably greater. It seems to be this latter fact which exerts its influence on the neritic larvae, where local differences in the water may often be limited to small areas, but may at the same time be rather considerable.

Pigmentation.

In most Crustacean larvae the red pigment is more or less pronounced. When present, the pigment is, as a rule, placed in such characteristic chromatophores that they may often be of great help in distinguishing the different species of larvae from each other. However, the pigment disappears on preservation of the larvae, and often when the larvae does not thrive well the pigment may disappear already some time before its death. I have collected larvae which on arrival at the station were in such a poor condition that they were completely without pigment. The pigment reappeared however, after the larvae had been kept in darkness and at a temperature of 3—4° Centigrade for some days. In those larvae which recovered completely the pigment was found in large characteristic spots in places in which, on arrival of the larvae to the station, it had been impossible to ascertain the presence of any pigment even under the

microscope. For the sake of completeness it should be added that in several of these specimens the pigment was observed in the fishing place immediately after they had been caught, but although the material was transported to the station in thermo-flasks, several of the larvae were in such a poor condition on arrival at the station especially in hot weather that, as already mentioned, they had completely lost their pigment. As my observations on the pigmentation of the larvae differ somewhat from what is stated in the literature, I shall at first call attention to the facts that in the Gullmarfjord *Meganyctiphanes norvegica* lives near the bottom of the fjord, separated from the open sea by a sill across the mouth of the fjord. For these reasons we may regard it as absolutely certain that the larvae of no other Euphausiacea occur in this locality.

The *Meganyctiphanes* larvae have been described, more or less completely, four times in the literature. The first time by Sars (1898). He does not say very much about the pigmentation, he states, however, about the first Calytopis (pp. 29, 30) that "a light red diffuse pigment has appeared in some places, especially in the region of the mouth." Regarding the following Calytopis stages he says that there is further found a faint red pigment on each side of the eye plate. The next paper is that of Lebour (1924). Here we get a somewhat more detailed description of the pigment and its distribution. Lebour found that in the egg the Nauplius assumed "a pale pinkish colour". About the first Calytopis she says (p. 414): "The first Calytopis of *Meganyctiphanes* is pinkish in colour with bright orange-red pigment diffusing outwards from two chromatophores in the thoracic region. Sometimes there are two pairs. Pigment is also present in the mouth region, and dorsally all along the body there is a diffuse pink shade. There are, however, no chromatophores on the telson as there are in *Nyctiphanes*, and by their pigmentation the species can be at once distinguished." This description is cited in extenso because it differs in essential points from the results to which I have arrived. Later (1925, p. 822) however she writes that "the early larvae of *Meganyctiphanes* may have a trace of red chromatophores at the base of the telson." Lebour further states that living *Meganyctiphanes* always show a pink colour all over the body, which make them easily distinguishable from other species. In the later work by Macdonald (1927) no further account is given for the pigmentation. Einarsson (1945, p. 22) mentions the statements about the pigmentation given by Lebour (1924), but he has overlooked the partly revised statement (1925, p. 822), and, unfortunately, it is the incorrect information about the tail pigment to which Einarsson paid attention.

But let us attempt now to compare these statements with the results to which I have arrived in my investigations. Figs. 1—6 show the eggs in different stages of development. It is seen that the unicellular, newly-spawned eggs apparently possess no pigment, but as the eggs are developed, the pigment begins to be formed, partly as a waste-product from the metabolism. At first the pigment appears quite diffused, as seen in Fig. 2, but in the Gastrula stage (Fig. 3) the pigment tends to gather somewhat more densely round the primordial mouth. When the Nauplius is being formed inside the egg, the pigment mainly appears at the apex, situated principally in the posterior end of the Nauplius. Figs. 4—6 show the same egg seen from different sides. It is seen how the Nauplius limbs are being formed and how the pigment is gathered round the apex. But this pigment appeared as sharply limited grains; I never observed any eggs or larvae of a pink colour, as recorded by Lebour, except when the eggs or larvae were dead or dying. In that case the pigment was soon dissolved in the body fluid and gave to it a pinkish tinge. The term 'dying' should not here be taken too strictly for I have seen larvae lying apparently lifeless on the bottom of the jar, and, only occasionally slight

movement of one of the limbs was seen and, in periods with long intervals, faint contractions of the heart. Such "dying" larvae could live in this state for 3 or 4 days, and in certain cases the pigment had been dissolved in the body fluid at this stage, so that the entire animal had a pinkish tinge. But such specimens never recovered, even when tended with the utmost care, as far as this was possible.

Simultaneously with the development of the animal the pigmentation increases. In the free Nauplius stage (Figs. 8—9), as in the Nauplius in the egg, the pigment in the abdomen is first seen, but in addition the upperlip or labrum has now also begun to get a faint layer of pigment near its free outermost edge. Further it is seen on both figures that the so-called Nauplius-eye has begun to form in the usual way as a double eye with the two pigment cups turning the convex side towards each other. This development is continued in the Metanauplius (Figs. 10—12). The double eye-cup is seen distinctly in Fig. 10. At the same time this figure shows that the pigment of the abdomen is now found in two groups in that part of the abdomen from which the future tail-plate is to be formed.

In passing from the Metanauplius to the first Furcilia stage, a change as well as a steady increase in the amount of pigment has taken place. Besides the Nauplius-eye now the lateral eyes of the adult have also begun to develop, and in the middle of these lateral eyes a gathering of red pigment takes place (Figs. 13—15). But also the abdominal pigment has undergone some alteration, the two groups being now divided into four, or two pairs, as is distinctly seen from Figs. 13 and 17, both figures representing the first Calytopis stage. The most anterior of these pigment spots is situated outside the lateral spine of the tail, while the next pair is found posterior to these, farther out in the future telson.

In the second Calytopis stage (Fig. 14) the pigment of the upper lip has developed strongly, so that we now find the labrum as a big red flap in front of the mandibles. Also along the lateral edge of the carapace a faint pinkish tinge has begun to show. This latter, however, appears to be due to the internal organs, e. g. the hepatopancreas, which is beginning to be formed, rather than to distinct grains of pigment, as has otherwise been the case. This is also seen in the first Furcilia stage, just as here, also, the lower lip has been pigmented. Figs. 32 and 33 show the distribution of pigment in the upper and lower lips of the first Furcilia stage. From the third Calytopis stage (Fig. 15) the uropods are developed and the telson is divided off from the abdomen. In the telson the double set of telson pigment is distinctly observed. It is preserved through all the part of the development which I have been able to follow, viz. the fourth Furcilia stage inclusive. Everywhere in the telson the free pigment spots are seen which during the development move farther apart so that the most anterior pair, though situated on the telson itself, is found beneath the uropods, while the most posterior pair moves backward towards the posterior edge of the telson plate. This development is distinctly seen in Figs. 17 and 18, representing the first and third Calytopis stage respectively, and in Figs. 19—21 which represent the telson in the first to third Furcilia stages.

While the different organs generally increase in size during the development, this does not hold good for the Nauplius eye or the median eye. In Figs. 13 and 14 it is seen to lie relatively free in the first and second Calytopis stages, but in the third Calytopis stage it begins to become squeezed in between the two lateral eyes, and in the first Furcilia stage (Fig. 16) it is completely hidden by these latter eyes.

Abdomen and telson.

In the Metanauplius (Figs. 10, 12) the abdomen is as yet only represented by a small bud protruding backwards from the carapace, but already in the first Calytopis stage the abdomen is extended so as to attain a length equal to or even surpassing that of the carapace, but the entire abdomen is still completely unsegmented, also the telson has not yet been divided off from the abdomen.

In the second Calytopis stage the abdomen is further extended; in certain individuals a segmentation of the abdomen may have taken place at this stage, but in the greater part of the specimens investigated by me this segmentation did not take place until in the third Calytopis stage. In that stage the abdomen may be divided into from four to six segments, the general rule being, however, that six segments are not found until in the first Furcilia stage. In the following, the second Furcilia stage, the abdominal limbs or the pleopods begin budding from the abdomen. There is, however, a possibility that the pleopods are beginning already to appear in the first Furcilia stage, but, as previously mentioned in the chapter about the larval stages it may hardly be regarded as of common occurrence and, at least, it was not the case in any of the specimens investigated by me.

In comparing these results with the results of Fraser (1936) and Einarsson (1945) it must be remembered that both these authors, in contrast to most other investigators of the Euphausiacea, have numbered the telson as a separate segment, and thus they get one segment more. Not very much will be said here about the telson. We have already discussed the telson-pigment and need only briefly mention the telson itself. The beginning of the telson may be ascertained in the Metanauplius (Figs. 10—11), but, as mentioned above, it does not become divided off from the abdomen until in the third Calytopis stage. In the first stages after the division from the abdomen the third Calytopis and the first Furcilia stage is rather hour-glass-shaped (Figs.18—19), while in the following Furcilia stages it becomes longer and more slender (Figs. 20—21).

Regarding the telson spines we find that the lateral tail spine appears already in the Metanauplius (Figs. 10—11). It grows almost to its full size during the Calytopis stages, so it appears to be relatively "over-sized", but it does not develop further in the following stages and on this account now appears to be considerably smaller. Also the spines on the posterior edge of the telson begin to develop in the Metanauplius stage. Three well developed backward-directed spines (Fig. 11) are found in this place, and inside these are two incipient spines. This spinosity becomes further developed in the first Furcilia stage (Fig. 17). It is here seen that the two most exterior spines are quite smooth, then follows a spine which is smooth on its lateral edge but dentate on the edge towards the medial side. In these three spines the length increases from the outer towards the inner spine. Then follows some short, stiff, plumose spines. Lebour (1925, pp. 814—815) states the number of these to be seven, but adds that in another form, *Stylocheiron suhmii*, they are found in a number of six only. Macdonald (1927, p. 788) shows that the median seventh spine is suppressed in several species of Euphausiacea, mainly in the first Calytopis stage, after which it may develop in later stages. He thinks that this feature indicates a close relationship between the Euphausiidae and the primitive Decapods. Einarsson (1945) records six spines in the first Calytopis stage of *Meganyctiphanes*, seven spines in the following stages. I can here in the main agree with Einarsson that there are six spines in the first Calytopis stage. However, my material shows that the seventh spine does not always

appear in the second Calytopis stage, and in certain cases not until the third Calytopis stage, which, according to my experience, always carries all the seven spines (Fig. 18). As seen from this figure, the median seventh spine is somewhat shorter than the others, the same is the case in the following two Furcilia stages (Figs. 19—20); not until in the third Furcilia stage (Fig. 21) are all the seven spines of the same length, their points forming an even curve parallel to the posterior edge of the tail-plate. Figs. 19—21 show at the same time that the exterior pair of the thirteen spines of the distal edge of the tail-plate become shorter and shorter from the first Furcilia stage and onwards, being, already in the third Furcilia stage, reduced to a pair of tiny, short spines.

Luminescent organs.

The luminescent organs, so characteristic of the Euphausiacea, do not appear at once in the youngest larvae, but develop, at the earliest, in the Furcilia stage III. Quite exceptionally, however, one may be able to observe a faint, still unpigmented, incipient stage of the luminous organs in the Furcilia stage II. In both cases we are concerned with the luminous organ of the first pair of pereiopods after the maxilliped (Fig. 37). The incipient organ at first begins as a faint ring, but soon becomes more strongly pigmented, as shown in Fig. 37, which shows one of the larvae with the most developed pereiopods and luminous organ found in this stage. At the same time the unpaired abdominal luminous organs likewise begin to be formed in a successive series from the anterior end and backwards, so that the anterior organs become the most advanced in development, as shown in Fig. 40, a figure drawn after a larva in the fourth Furcilia stage; in some cases they may, however, be somewhat more developed in this stage, just as the figured stage of development may be found in larvae of the third Furcilia stage. At last, also, the luminous organ are strongly pigmented, as shown in the figures, and the amount of the pigmentation increases according to the degree of development of the organ and the age of the larva.

The Mandible.

The mandible as it develops in *Meganyctiphanes* may be interpreted in different ways:

I. The corpus mandibulae is usually looked upon as one and the same thing in all arthropods. In the *Calanidea*, among the free living copepods, it can easily be seen that the corpus mandibulae is formed by and from the first joint of the limb, which was termed coxa by most authors, but precoxa by HANSEN who took the sympod to consist primarily not of two, but of three joints, and as the corpus mandibulae was still the first joint of the limb, it must, according to HANSEN, represent this newly detected joint, which he named precoxa. But if the larval development of the mandible of the *Calanidea* is taken in account, we see that the intermediate or second joint of the sympod in the mandible is not a real joint, but only a secondary joint. This means that the mandibular sympod of the *Calanidea* has only two real joints and therefore no precoxa is found in the calanid mandible, the first joint being the coxa (see HEEGAARD 1947, b.). Further, if the mandible possesses a palp, as is the case in several *Crustacea*, this must be formed by the rest of the sympod, which means, according to HANSEN's interpretation, the two following joints: the coxa and the basis; most other investigators interpret

the corpus mandibulae to be formed from the coxa, thus there is only the basis left to form the palp. If there are more joints in the palp, the following joints represents the endopod.

This is the usual way of interpreting the mandible throughout the crustacea, but it is difficult to fit all mandibles into this scheme. It must also be remembered that only in the *Calanidea* and in a few *Harpacticoidea* (both Copepoda) is the entire mandibular limb to be found in the adult, and in most cases the reduction is evident in the larva when it is hatched. Therefore, without drawing any comparison or homology from the *Calanidea* to the *Euphausiacidae*, a second interpretation may be taken into consideration.

II. It is a commonly known feature of the morphology of the *Crustacea* that when a swimming limb or a swimming branch is to be formed, it is nearly always formed by the exopod. We must here disregard such cases as the flattened swimming limbs of certain species of crabs, these limbs being actually ambulatory limbs which are secondarily used for swimming; and as the crabs at a much earlier stage of their developmental history have lost their exopod, this, according to Dollo's law cannot reappear. As I have already pointed out (1947b) the function of the palp on a limb is exactly the same as that of a swimming limb. It is only a relative difference whether the surrounding water should be moved in relation to the animal by the aid of the palp, or whether it is the animal itself which by means of the swimming branch should be moved in relation to the surrounding water.

If this fact is taken into account it will be seen that there is a second interpretation of the palp of the mandible in *Meganyctiphanes* which can be fitted to the facts we know about the development of the mandible. When in 1945 (p. 7) I attempted to show the variation of the mandibles of the *Mandibulata*, I tentatively suggested that the mandible of the *Malacostraca* may be interpreted in the following way that the peduncle of the mandible plus the pars molaris is derived from an unsegmented sympod, and that the palp consists of the endopod, while the pars incisiva, if present, is formed by a gnathobase from the first joint of the endopod. I had arrived at this possibility by considering the variation found in the shaping of the mandibles in the copepods, but the present investigation of the development of the *Meganyctiphanes* shows that this explanation is wrong.

In the Nauplius (Figs. 8—9) the mandible is still the typical swimming limb with a strong unjointed sympod, an exopod, and an endopod. Both these latter are likewise unjointed. In Fig. 9 the Metanauplius is seen beneath the skin, and it can be seen how the mandible of the Metanauplius is situated inside the sympod of the Nauplius mandible. In Fig. 10 it is shown that in the Metanauplius the mandibular sympod grows in an arch towards the median line of the animal, where it terminates in a tooth-bearing part on which the teeth are situated in several rows behind each other (S. in Figs. 22, 23, 24 and 25). It appears that the chitin of the sympod is deposited in several layers, one upon the other, in such a way that each layer terminates towards the apex in a row of pointed teeth. The outermost layer is the shortest, and only the interior layers reach as far forward as to meet from both sides. The teeth are arranged in an amphitheatre-like way. This part, termed Pm. in the above mentioned figures and generally described as pars molaris of the mandibles, is thus in direct connection with the base of the mandible without any division in the form of a suture, segment limit, or anything else; and in no period of the development, or in the adult, do we find any discontinuity in this part. We may therefore rightly consider this total part as representing one joint.

From this joint issue two branches termed (in Figs. 22—25) Ex. and En. respectively. Thus we actually have a bifurcated appendage, although in a somewhat transformed shape.

As all who have described the mandibles of the Nauplius agree that it has an unsegmented sympod carrying an unsegmented exopod and endopod, there may be some reason to suppose that the sympod remains unsegmented. There does not seem to be any evidence in the Euphausids to indicate the contrary. But if this is the case, the sympod, then in the still unsegmented form, is turned inwards and by its distal dentate edge forms the molar part of the corpus mandibulae. The branch on the lateral side of the mandible body (Ex) must then be the exopod. The endopod may be interpreted in two different ways, either that the endopod is lacking, and the incisor part of the mandible is only a part of the sympod, which in the younger stages has a definite marginal line (Fig. 22—23) towards the molar part of the mandible, or that the incisor part of the mandible represents the endopod.

However, the later exopod and possibly the endopod, are not formed inside the exopod and endopod of the Nauplius before the ecdysis, but since considerable shortening of the length of the sympod takes place at the metamorphosis from the Nauplius to the Metanauplius, the exopod and endopod will again bud off from this shortened sympod. If we want to fit this transformation into the terminology, we may name the new exopod and endopod the secondary exopod and the secondary endopod respectively. But how are these two branches formed here in the mandibles? The branch which according to its position must represent the exopod is still only a small knob on the sympod. All the figures (Figs. 22—24) show distinctly that this knob is placed directly on the sympod, having no connection with the pars incisiva (Pi in the same figures). I have figured the mandibles in different stages, from the third Calytopis to the third Furcilia stage and viewed from different angles, in order to make it clear to the reader that this knob has nothing at all to do with the pars incisiva, a fact which, as we shall presently find, may be rather decisive for our entire conception of the mandible. The exopodial knob develops into the palp, which in the adult usually consists of three joints. The further development of the palp of the mandible is illustrated in FRASER's figure of development of the mandibular palp in *Euphausia superba* (FRASER 1936, fig. 8.).

The incisor part of the mandible (Pi. Figs. 23—25) is then either formed from a part of the sympod or it represents the endopod. This branch is a continuation of the sympod, as is usually the endopod. It may be remembered that there is not even a division between sympod and endopod in the limb of the Anacostracan Crustacea. The edge of the pars incisiva is produced into large saw-like teeth. During the growth of the larva this pars incisiva begins to turn in another plane from the rest of the mandible and assumes a more arched shape (Fig. 25).

The description of the mandible of the *Euphausiacea* may be summed up as follows: Either, I, the corpus mandibulae represents the coxa, and the rest of the limb forms the palp, or, II, the mandible consists of an unjointed sympod which forms the mandibular peduncle and the pars molaris. The pars incisiva is either a part of the sympod or formed by the endopod (secondary endopod) and the palp is the exopod of the limb (secondary exopod).

The Maxillae.

As is well known, there are two pairs of maxillae, the first and the second pair.

First maxilla. (Figs. 14, 16, 26, and 28). The understanding and interpretation of the first maxilla have given rise to a great many difficulties and some disagreement in the literature. Boas (1883) was the first to attempt to solve the problem of the mouth appendages of the Crustacea on a comparative morphologic basis. As it was the first work of this kind on the Crustacea we must regard it with admiration. Many views, which to-day seem so evident that nobody will ever think that they might contain problems, are here set forth for the first time. Of course, Boas also set forth some wrong conclusions, but this can hardly be avoided in such pioneer works on natural science as his two works on Crustacea (1880, 1883). In his work of 1883 (p. 495, fig. 41) Boas records for *Thysanopus* an exopod and a two-jointed endopod issuing from the second joint. This is in itself correct, but his first joint is merely a secondary sclerite, and his second joint is thus actually the first joint of the appendage; at the same time he overlooks an intermediate joint from which his lacinia interna is formed.

Sars (1885, 1895) writes (1895, p. 33) about *Meganyctiphanes*: "The anterior maxillae consists each of 3 principal parts, viz. the basal part, the palp, and the exognath. The basal part is apparently composed of 2 imperfectly defined segments . . . the palp is composed of two flattened joints." Further Sars found (1885) that the part of the appendage which is sometimes termed the palp, sometimes the endopod, was unjointed in all the stages of the two species *Nyctiphanes australis* (p. 154) and *Thysanopoda tricuspidata* (p. 166) found by him.

In contrast to Sars' two-jointed palp in the *Meganyctiphanes*, Lebour found this palp to be unjointed in *Thysanoessa inermis* as well as in *Meganyctiphanes norvegica*. In 1926 (p. 5) Lebour writes further about *Thysanoessa inermis*. "The endopodite of the first maxilla is, however, in one piece and not two-jointed as in a figure of a Calytopis figured by Hansen (1925) which he regards as a *Thysanoessa*, and which he says becomes unjointed in a later stage." Calman (1909, p. 245) says about the Euphausiacea in general: "The maxillulae have the usual two endites and a palp which is generally unsegmented, but has three segments in *Benteuphausia* and two in some larvae. An exite of the third segment (exopodite) is present in the larva, but is replaced in the adult by an exite of the first segment, sometimes erroneously called the exopodite."

Hansen (1925, p. 127) finds the sympod to be three-jointed, while the endopod is one-jointed except in *Benteuphausia;* the second joint carries a big lobe (Boas' lacinia interna). The basis or the third joint of the sympod forms a large plate (Boas' lacinia externa).

Rustad (1930) briefly summarizes the diverging opinions, but he dares not himself decide the question on account of the state of his material. Fraser is just as cautious, omitting to draw the inner limits of the joints in his figures of the maxillae. The same applies to Lebour's and Macdonald's figures of the larvae. As will be seen, there is a great confusion, no two interpretations being alike. It is therefore with some hesitation that I add one more interpretation to the literature, still I do it, partly because I am the only one who has followed the development from the Nauplius and may discuss the problem on that basis — this having not been done by the only three authors, Boas, Calman and Hansen, who have attempted to interpret all the parts of the appendage as a whole — and partly because during my thorough study of the appendage I have arrived at a solution which, though it differs essentially from the results reached by these three authors, has the advantage that it shows the maxilla to be actually a crustacean appendage much less transformed than has hitherto been supposed.

In order to understand how the appendage is built up we will begin at its first appearance in the Metanauplius (fig. 10), where it still has an exceedingly embryonic character. But in the following Calytopis stage it has already attained the appearance of a normal bifurcate appendage. Fig. 14 shows the second Calytopis stage. It is seen that the first maxilla has a two-jointed sympod, the two joints of which, the coxa and the basis, are of almost the same size and appearance. On the sympod there are also an exopod and an endopod, both unjointed. Passing on to the first Furcilia stage, we shall see that the appendage has already developed considerably (Figs. 16, 26). In the latter figure the appendage is shown in detail. The sympod still consists of the coxa and the basis; the latter has begun to broaden and to form a lacinia, the future lacinia interna. That this lacinia is formed by the basis, may be ascertained by a close observation of the appendage, which will be found to carry two branches, a three-jointed and a two-jointed one, the three-jointed one being the exopod. It will be seen that the first two exopodial joints each carry one seta, while the distal, third joint is provided with two setae. This may probably indicate that the exopod was originally four-jointed, with a seta for each joint. The difference in this respect from the results of all the earlier investigators is partly that the exopod was found to be three-jointed, partly that it originates from the joint which later on forms the lacinia interna. According to the earlier authors the exopod originates from the following joint, which is to form the lacinia externa. However, it should be added here that HANSEN is the only one who has shown the limits of the joints in the maxillae of the larvae. The difference between HANSEN's and my results must undoubtedly be due to the fact that HANSEN made no special investigation at such an early stage of the larval development. For, later in the development, when the exopod degenerates, it moves at the same time towards the first joint of the endopod, or the lacinia externa, and it moves so close towards it that it may easily be overlooked that the exopod extends right down on to the lacinia interna. The second branch of the appendage is the endopod. In fig. 26 it is seen that in the first Furcilia stage there is a rather wide distance between the places of origin of the exopod and the endopod. The endopod, as shown in the figure, consists of two joints, of which the first is larger, obliquely placed and provided, on its medial edge, with some peculiar dentate setae. The first endopodial joint gradually becomes more strongly developed in a medial direction, and is later transformed into the so-called lacinia externa. From its lateral edge originates then the following, second endopodial joint. As appears from the figure, the longitudinal axis of this joint thus runs almost parallel to that of the exopod. This joint is the one which has usually been termed the palp, and which has hitherto been recognized as the only endopodial joint of the appendage; further it is about this part of the palp there has been so much discussion as to whether it has one or two joints. It is seen from the figure that in the specimens investigated by me this part of the palp has only one joint; yet, a distinct notch was found behind the second seta, this notch much resembling a rudiment of a previous limit of a joint. It is possible that it may be such a notch which was taken by SARS and others to be a genuine limit of a joint, but in the specimens investigated by me only the one notch figured was found.

The appendage just treated must in every respect be conceived as an only slightly transformed bifurcate appendage, but it differs in very essential characters from the descriptions hitherto given of the first maxilla. However, let us follow the further development of the appendage.

We will now proceed to the last of the larval stages I had the opportunity to investigate, viz. the fourth Furcilia stage (Fig. 27). It is here seen that the coxa has been reduced and now forms merely a base or an incipient peduncle for the following joint, the basis. This latter

joint has been provided with more, but at the same time stronger and shorter, setae than it had in the first Furcilia stage. The future lacinia interna is about to take shape. The exopod, which has now moved quite close to the first joint of the endopod, has been reduced from three to two joints. From the number of setae and their places on the joint it may be concluded that it must be the distal joints which have become fused into one. During the following development the two remaining joints, also, become fused so that we finally get the unsegmented exopod with four plumose setae known from the literature.

If we now pass on to the endopod, it will be seen that its first joint begins to form the lacinia externa. Here, also, an increase in the number of setae has taken place. These setae are usually very strong, forming the beginning of the later so strongly dentate medial edge, while the rather stiff setae, which afterwards cover this row of teeth, have not yet been developed. The outline of the following, the last, joint of the endopod has not undergone any essential change, but while formerly it was turned laterally outwards, towards the exopod, it is now turned towards the medial plane, away from the exopod.

Unfortunately, as already mentioned, I did not have the opportunity of following the larval development any further, but the transformation is so far advanced that by the aid of the figures in the literature we may without difficulty see the connection with the first maxilla of the adult.

All the investigators of the larval forms have hitherto figured the exopod as consisting of one joint bearing four plumose setae. Thus we know that a further reduction takes place within the exopod, so that the two joints finally become fused into one joint. Besides, both Hansen and Fraser have shown in their papers that the exopod of the adult is not identical with that of the larval form, but is a so-called pseudo-exopod, which begins to be formed before the original exopod has completely disappeared.

With these remarks as an introduction we may now attempt an interpretation of the fully developed first maxilla of the adult (Fig. 28). First we observe that the coxa has been further compressed and now lies as a peduncle-like piece proximal to the maxilla proper. At the end of this joint is found a faint suture (dotted line in the figure) so the proximal point may be conceived as a secondarily split from the precoxa. Then comes the basis, carrying on its flattened lateral side the pseudo-exopod, which is an elongate, flat, membraneous leaflet with a series of short setae in its distal rounded point. The basis itself is further widened into a medially running lobe, the so-called lacinia interna. From the lateral axis of the appendage issues also, from this joint, the two-jointed endopod, the first joint of which is likewise widened into a medially directed lobe, the lacinia externa, which, as will be seen, is now provided with both a dentate edge and a series of setae covering this edge. Then follows the second and smaller joint of the endopod, "the palp", carrying a comb of dense, plumose setae.

These are the main joints of the appendage, but besides there are a sclerite (Fig. 28 sc) reaching from the precoxa to the basis. In order to understand this structure we must think of the development of the limb. Originally we had a normal bifurcate appendage issuing from the body at a right angle. During the development the appendage becomes strongly flattened and at the same time it is turned forwards, towards the body, so that it comes to lie close against the latter. The mobility of the appendage has not been reduced during the turning, on the contrary it has been strongly increased on account of a strong development of the muscles, especially those which move the appendage in relation to the body. In order to make room for these muscles the exterior lateral side, at the place where the appendage joints the body, has been pushed outwards, one might say that the skin of the joint has been stretched

considerably to provide room for the muscles. Then, secondarily, a sclerite plate has been formed to protect the muscles and support the skin. This sclerite, however, only covers the lateral convex part of the articulate surface.

Thus we get a three-jointed sympod, the third joint of which, the basis, forms the lacinia interna, while the lacinia externa is formed by the first endopodial joint, the second endopodial joint forming the so-called palp. Further the exopod has disappeared and has been replaced by a pseudo-exopod. Finally a secondary sclerite is found, reaching from the precoxa to the basis without being firmly connected with either of these; this sclerite, too, lies quite superficially on the lateral side of the appendage and does not continue in a ring over the medial side.

Second maxilla. This limb is of a much simpler structure and has, therefore, never given rise to any great difficulties. Boas (1883) initially described it as having a two-jointed sympod, each of which joints formed the lacinia interna and the lacinia externa respectively. Further, the second joint carries an exopod and an endopodial palp. Calman (1909) follows Boas, but adds that there is a joint proximal to Boas' first joint, stating (p. 246) "that the maxillae (Fig. 140 C) generally consist of four segments; the second and third have each two endites." But in Calman's figure this first joint mentioned by him is not shown. Hansen (1925, p. 127) was the first to describe and figure this third joint, saying "The maxillae are completely plate-shaped and consist of a three-jointed sympod, a quite short and very broad exopod...., and an endopod."

In this I can agree, though with some modification. If we want to get the right understanding of the precoxa, which Hansen interpreted as the most primary part of the appendage, we must examine the development of the appendage.

Here, also, we may begin with the Metanauplius. The second maxilla, like the first maxilla, is here still an embryonic appendage (Fig. 10), but it develops rapidly, and in the first Calytopis stage it has already become a well developed bifurcate appendage. Fig. 14 shows it in Calytopis II. It is seen to consist of a two-jointed sympod, with two branches coming from the basis, an exopod and an endopod, both still unsegmented. Fig. 16 shows it in the first Furcilia stage. In Fig. 30 it is shown in detail.

It is seen that the sympod at this stage has still only two joints, and that at this stage the appendage has already begun to flatten out, just as the two lobes has begun to develop. The first of these, the lacinia interna, is already beginning to become two-jointed. The appendage is divided from the basis into two branches, the endopod, which in this stage forms a third lobe, and the exopod, which, like that of the first maxilla, is three-jointed. In the figure the first endopodial joint is seen to be rather short and without setae, the second and the third joint being both more elongate and each provided with three strong setae. On the second exopodial joint there is further a shorter and more slender plumose seta distally on the lateral side.

For comparison it may be mentioned that Fraser says as follows about the second maxilla of the first Furcilia stage (1936, p. 73). "The 2nd maxillae are as in the 2nd Calytopis stage with five lateral lobes bearing many setae and a terminal lobe with three setae." This corresponds to what I have found, only with the difference that Fraser has not seen that these lobes are formed partly by a sympod and partly by an exopod and an endopod. This division of the appendage into an exopod and an endopod was overlooked by Fraser, but the two branches lie indeed so close to each other, that only on careful examination will it be seen that these distal lobes are found on the peduncle and are accordingly different branches of the appendage.

Until the fourth Furcilia stage no essential transformation of the second maxilla takes place. Unfortunately for several reasons I have been unable to follow the development any further, which is regrettable.

In the literature the exopod and the endopod of the young larvae have not been acknowledged, but it is said that an exopod appears later, at first as a small bud, which later develops into the leaf-shaped exopod of the adult, which in all essentials is built like the pseudo-exopod of the first maxilla. These facts indicate that the three-jointed exopod, which remains as such at least to the fourth Furcilia stage, is reduced and gradually disappears during the development, to be replaced by a small bud, which later develops into the leaf-shaped exopod of the adult; this exopod of the adult is accordingly to be regarded as a pseudo-exopod, like in the first maxilla.

As regards the second maxilla of the adult I have nothing to add to the usual description of the coxa and the basis, each of which is divided into two lobes, and, uppermost in the appendages, the single endopodial lobe. We have seen that the "exopod", like the "exopod" of the first maxilla due to its development must be regarded as a pseudo-exopod. There remains, then, the precoxa. Previously in my paper of 1945, and especially 1947 b, I have shown that the precoxa, if present, is not a primary formation, as was the opinion of Hansen, but a formation of an extremely secondary character. We note here, also, that the sclerite (Fig. 31 Sc.), termed the precoxa by Hansen was not found in any of the larval stages studied. It is further noticed that like the sclerite of the first maxilla it has a relatively free position in relation to the rest of the skeleton of the appendage, and it is likewise only found on the lateral articular surface of the appendage towards the body, its function there being the same. Apparently the only difference is that while the sclerite of the first maxilla proved to be an entirely new formation, the sclerite of the second maxilla, judging by its outline, appears to have been split off from the coxa, after which, on account of the further growth of the connecting muscles, it has been pushed away from its contact with the remaining coxa, except in a small area on the lateral side of the appendage. There appears thus to be a reasonable justification for terming the sclerite the precoxa, as long as it is remembered that this does not mean that it is of a primary character; on the contrary, it is a secondary formation.

Phylogenetic remarks. In 1926 Scourfield described a new Cambrian Crustacea, *Lepidocaris rhynensis*. This discovery, as pointed out by Calman 1926, was one of the most important contributions to the understanding of the morphology of the arthropods.

One of the most difficult problems of crustacean morphology has been the correlation of the biramous type of limb found in most Crustacea with the 'phyllopod' type seen in the Branchiopoda. But in *Lepidocaris* both types of limbs are found. The first three pairs of thoracal limbs are phyllopodial and the following pairs are biramous. From this Calman draws the conclusion that the biramous limb must be the most primitive, and that it is likely that *Lepidocaris* had primitively biramous appendages of which the more anterior had become foliaceous by specialization. This point of view was further strongly supported in a later paper by Scourfield (1940), in which it was shown that the first one or two pairs of trunk limbs in the younger Lepidocaris stages — with eight and nine somites — were much simpler and much more definitely biramous than in the adult.

In my papers of 1945 and, especially, 1947 b I gave further proof of this point of view. In the maxillae of *Meganyctiphanes* we have another example of a bifurcate appendage which is transformed into a phyllopodial-like appendage. It was found that the maxillae in the Caly-

topis stages began as entirely bifurcate appendages, and that during the development the appendages were flattened out; endites were formed in the shape of the lobes: the lacinia interna and the lacinia externa; even exites were formed, the exopod being substituted by a pseudo-exopod, which in all essentials was built like exites of the phyllopodial appendage. Against this it may presumably be objected that the phyllopodial appendage of the Phyllopods ontogenetically does not begin as a real bifurcate appendage. This is only partly correct, for, as mentioned above, in Lepidocaris the first three thoracic appendages at first develop as bifurcated limbs which are subsequently transformed into the phyllopodial type. This is a very interesting point, as it is precisely the same which happens to the maxillae in the recent Euphausiacea. Further the argument that the phyllopodial appendage of the recent Phyllopods never resembles a bifurcated appendage, is not quite correct either, the swimming appendages of the Anacostraca at first having a peduncle carrying three medial lobes and, issuing from the distal part of the peduncle, further two lobes, and it is precisely these two lobes which develop into the exopod and the endopod of the appendage. In the Anacostraca, as also in a few other Crustacea, we find an interesting reversible process in the development of the appendages. I am here referring to the second antenna. In the Anacostraca it has at first an unjointed sympod, which, however, at an early stage of development becomes divided into two joints, the coxa and the basis. This bisegmentation is maintained throughout the entire larval life, but when the animal attains sexual maturity, the function of the second antenna is about to change from being an important — at first the most important — means of locomotion, to function, in the male, as a prehensile appendage, by means of which the female is grasped during the act of fertilization. During the transformation of the second antenna, which follows upon the transition to this new function, the coxa and the basis again fuse to form the peduncle of the antennular tongs, while the blade is formed by the exopod.

The Maxilliped.

The first pair of limbs after the maxillae were regarded by Calman as ordinary thoracic limbs. He states as follows (1909, p. 246): "None of the thoracic limbs are specialized as maxillipeds, the first pair being similar in structure to the succeeding pairs." This point of view has been followed by most authors of the Euphausiacea, also by students of the larval stages. But Hansen terms the first pair of thoracic limbs the maxillipeds. The first point of view that there are no maxillipeds, which was originally set forth by Boas (1883), may appear to be correct as long as we only consider the adult specimens, for in this case there is only little difference between the first pair of thoracic limbs and the succeeding pairs, only the first pair is smaller and more reduced than the following pair. But if we look at the development, we shall find that in the Metanauplius the first thoracic limbs are already formed, together with the mouth appendages before any other limbs are formed; furthermore these are the only limbs present through all the three Calytopis stages, and when at last, in the Furcilia stages, the pleopods begin to develop, this takes place before any of the pereiopods have been formed. This shows that the first pair of thoracal limbs now develop rhythmically along with the mouth appendages and no longer together with the following thoracal appendages. I regard this as sufficient justification for considering the first pair of thoracal limbs as maxillipedes.

This shows on one hand the primitive character of the Euphausiacea, on the other hand that the Euphausiacea have included the first pair of thoracal limbs among the mouth-appen-

dages, but have not yet transformed these, as have other forms with maxillipeds, in which they are shaped more like the maxillae than like the pereiopods. In the Metanauplius and until the second Calytopis stage there is no essential difference between the maxilliped and the preceeding maxillae. It is shown (fig. 10) that the maxilliped in the Metanauplius is merely a quite embryonal bifurcated appendage. In the Calytopis stages it has become more developed, and it is now, like the maxillae, provided with a two-jointed sympod, consisting of a coxa and a basis, and a one-jointed exopod and endopod. In the first Furcilia stage (fig. 29) it is seen that the coxa has developed a strong medial masticatory lobe with 8 plumose setae, and both the exopod and the endopod have now two joints. Later the limb becomes further developed, especially the endopod grows strong and helps, together with the other pereiopods, to form the "basket" by means of which the Euphausiacea catch and hold their prey. But, as is seen in these stages, the precoxa has not yet been separated.

Summary.

The present paper is based on an investigation of the ten earliest larval stages of *Meganyctiphanes norvegica*, performed at the Zoological Station of Kristineberg during the spring and early summer of 1947. The spawning commenced at the end of April, and was in full progress about the 1st May. The time interval from the spawning to the hatching appears to be 5—6 days at a temperature of about 4 ° C., while the first ecdyses took place at intervals of from 3 to 4 days. During the later development there was found to be an interval of from 7—8 days between the ecdyses, at the same time the temperature rose by some degrees.

It is shown that a stage — the first Furcilia stage without pleopods — occurs, although not found by Einarsson (1945) in his oceanic material. Furthermore it is shown that not only the pleopods but any organ of the animal may vary more or less within one and the same stage; as an example of this the variation of the pereiopods in a number of measured and investigated specimens is described, and textfigure 1 shows different developmental stages of pleopods, three non-setose and one setose stage. From this it appears htat in the "neritic" Euphausiacea there can be no question of fixed larval stages as in the higher Crustacea and Insecta, but that their growth and development must rather be considered as almost continuous, only retarded and partly interrupted by the necessary number of ecdyses. If it is correct that there is more stability in the development of the "oceanic" specimens than in the development of the "neritic" specimens, this may be explained by assuming that the conditions of development, good or bad, are more constant in the open sea than near the shore.

As regards the pigmentation it is shown that the red pigment gathers in the eyes, in the upper and lower lips, and in four characteristic spots on the telson. However, the pigmentation disappears when the animal does not thrive well, especially it disappears rather rapidly if the animal is kept at a too high temperature. This must be the explanation of the wrong statement that Meganyctiphanes, in contrast to Nyctiphanes, has no telson-pigment, a character which is repeatedly mentioned in the literature as the best distinguishing character between the larvae of these two genera. On the contrary the difference appears to be that Meganyctiphanes has four spots and Nyctiphanes, if the statement in the literature may be trusted, only two spots on the telson. The pink colour stated in the literature to occur all over the animal, was only observed by the present author in dead or dying specimens.

The luminescent organs of the eye-stalk, the pereiopod, and the first pleopod are often formed, but still only faintly pigmented, in the second Furcilia stage. In the third Furcilia stage these three luminescent organs become more strongly pigmented, and the luminescent organs of the second and the third pleopod are formed, but faintly pigmented. On the fourth and fifth pleopod the luminescent organs may be indicated as a faint ring, but still without pigment. However, as mentioned above, these developmental stages show individual variations.

The abdomen does not become segmented until the second or third Calytopis stage. The telson is not usually separated until the third Calytopis stage, that is, at the same time as the segmentation of the abdomen takes place. At this stage, also, the uropod is developed. The middle tail spines of the telson are at first only six in number. The seventh and most centrally placed spine appears in the second or third Calytopis stage, but does not attain the size of the others until the third Furcilia stage.

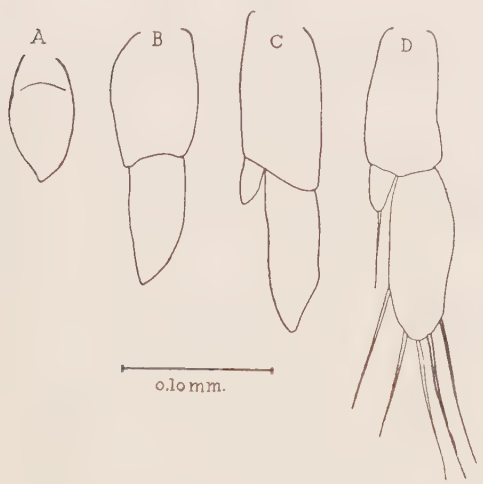

Fig. 1. Showing pleopod *A*—*C* all non-setose and therefore in their first stage of development. *D* pleopod in the second stage now setose. It shows the very great variation which can be found. *C* and *D* are nearly of the same shape only. *C* without, *D* with setae, and therefore an ecdyses has taken place between *A B C* on the one side, and *D* on the other side.

The development of the mouth appendages is followed in detail, and it is shown that the mandible of the adult may be interpreted as the following parts: the mandibular peduncle and the pars molaris formed by the sympod; the mandibular palp is formed by the secondary exopod, and the pars incisiva by the secondary endopod.

For the first maxilla it is shown that the larva from its first Furcilia stage has a normal bifurcated appendage consisting of a two-jointed sympod, a three-jointed exopod, which is placed on the second joint of the appendage, not the third, as hitherto assumed, and a two-jointed endopod. During the further development some changes take place. The first joint of the sympod, the coxa, gives off a precoxa. The basis develops into the lacinia interna, and the first endopodial joint into the lacinia externa, while the second endopodial joint is transformed into the so-called maxillary palp. The exopod becomes reduced segment for segment until its complete disappearance, and it is then substituted by the leaf-shaped pseudo-exopod. Finally, secondary sclerite from the precoxa to the basis is formed to support the locomotory muscles of the appendage.

The second maxilla is somewhat simpler, yet it exhibits some curious facts. At an early stage the sympod is divided into two joints, the coxa and the basis, which here during the development form the lacinia interna and the lacinia externa respectively. Thus it differs from the first maxilla, where the lobes are formed by the basis and the first endopodial joint.

The appendage further carries a one-jointed endopod, which later develops into the palp, and a three-jointed exopod. As in the first maxilla the exopod appears to be reduced and substituted by a pseudo-exopod. — Thus we have a pseudo-exopod both in the first and in the second maxilla. Finally, rather late during the development the coxa gives off a lateral sclerite, the so-called precoxa, which proves its secondary character by the way in which it is formed.

Then follows a general phylogenetic consideration in which it is proved that during the development the maxillae are transformed into typical phyllopodial appendages. Endites are

formed, the two laciniae, and the palp of the second maxilla, together with an exite, viz. the pseudo-exopod, and this is taken as a proof of the supposition previously put forward by the present author (1945, 1947 b) that the phyllopodial limb should be interpreted as a derivation from the bifurcated appendage.

Finally, the maxilliped is discussed. An argumentation by means of the ontogeny of the limb is set forth with the intention of reviving HANSEN's terminology for this appendage, viz. the first maxilliped, instead of the commonly used term, the first pereiopod.

Acknowledgement.

I express my most sincere thanks to the marine zoological station "Kristineberg", of the Swedish Royal Academy of Science, for very fine working facilities. I am also greatly indebted to the two Danish foundations, the Rask-Ørsted Foundation and the Carlsberg Foundation, whose grants made this investigation possible.

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Abbreviations.

A_1	First antenna	En	Endopod	Mx_1	First maxilla	Pl	Pleopod
A_2	Second antenna	Ex	Exopod	Mx_2	Second maxilla	Pm	Pars molaris
b	Basis	G	Gill-branch	Mxp	Maxilliped	S	Sympod
c	Coxa	LL	Lower lip	Pe	Pereiopod	Sc	Secondary sclerite
E	Nauplius-eye	Md	Mandible	Pi	Pars incisiva	UL	Upper lip

Dansk Resumé.

Dette Arbejde hviler paa en Undersøgelse af de 10 første Larvestadier af Lyskrebsen *Meganyctiphanes norvegica* foretaget ved Kristineberg zoologiske Station i Foraaret og Forsommeren 1947. I Slutningen af April begyndte Gydningen, og omkring 1. Maj var den i fuld Gang. Tiden fra Gydning til Klækning synes at tage 5—6 Dage, medens de første Hudskifter skete med 3—4 Dages Mellemrum. Senere i Udviklingen var der 7—8 Dage imellem Hudskifterne.

Udviklingsstadierne er følgende: 2 Naupliestadier, 1 Metanaupliestadie, 3 Calytopisstadier samt et Antal Furciliastadier. Det paavises, at ikke blot Bagkropslemmerne, men alt paa Dyret kan variere mere eller mindre inden for samme Stadie; som Eksempel herpaa vises de egentlige Kroplemmers Variation hos et Antal maalte og undersøgte Individer. Det fremgaar heraf, at vi hos Lyskrebsene ikke kan tale om fastlagte Larvestadier, som hos højere Krebsdyr og Insekter, men nærmest maa se paa deres Vækst og Udvikling som værende ret kontinuerlig, kun hæmmet og delvis afbrudt af det nødvendige Antal Hudskifter. Hvis det er rigtigt, at der er mere Stabilitet i Udviklingen hos »oceaniske« Arter fremfor hos »neritiske«, maa dette forklares ved, at Udviklingsbetingelserne, gode eller daarlige, er mere konstante i Oceanerne end inde ved Kysterne.

Angaaende Pigmenteringen vises, at det røde Pigment samler sig i Øjnene, paa Over- og Underlæbe, samt i fire karakteristiske Pletter paa Halepladen. Dog, Pigmenteringen er meget ustabil og forsvinder, saa snart Dyret vantrives; især forsvinder den ret hurtigt, hvis Dyret opholder sig ved en for høj Temperatur. Heri maa Forklaringen ses paa den i Litteraturen forkerte Angivelse, at Meganyctiphanes i Modsætning til Nyctiphanes ingen Halepladepigment har, en Karakter som i Literaturen stadig angives som det bedste Skelnemærke imellem de to Arters Larver. Forskellen synes tværtimod at være den, at Meganyctiphanes har fire Pletter og, om man kan stole paa Literaturen, Nyctiphanes kun to Pletter i Halepladen. Den i Litteraturen angivne lyserøde Farve over hele Dyret er af Forfatteren til dette Arbejde kun fundet hos døde eller døende Dyr.

Lysorganerne i Øjestilk og ved Grunden af Lemmerne er ofte anlagt men endnu svagt pigmenterede i andet Furciliastadie. I tredie Furciliastadie faar disse 3 Lysorganer kraftigere Pigment; Lysorganet ved andet og tredie Bagkropslem er anlagt, men svagt pigmenteret. Ved fjerde og femte Bagkropslem anes Lysorganerne som en svag Ring, men endnu uden Pigment. Der kan dog, som omtalt, være individuelle Forskelle i disse Udviklingsstadier.

Bagkroppen bliver først opdelt i Led i andet eller tredie Calytopisstadie. Halepladen afsnøres oftest først i tredie Calytopisstadie eller samtidig med Ledopdelingen af Bagkroppen; samtidig udvikles Halefoden. Af de midterste Haletorne paa Halepladen er der først seks; den syvende og midterste kommer frem i andet eller tredie Calytopisstadie, men naar først samme Størrelse som de øvrige i tredie Furciliastadie.

Kindbakkernes Udvikling gennemgaas, og det vises, at den voksne Kindbak er dannet af følgende Dele: Skaft og den knusende Tyggeflade dannes af Stammen, Ydergrenen danner Kindbakkens Palpe, og Indergrenen danner Kindbakkens skærende Del.

For Midtkæbernes vises, at Larven fra første Furciliastadie har et normalt Spaltelem bestaaende af en toleddet Stamme, en treleddet Ydergren, der sidder paa Lemmets andet Led og ikke som hidtil angivet paa tredie Led, samt en toleddet Indergren. Der sker da i Udviklingen en Del Ændringer. Stammens første Led, kaldet Coxa, fraspalter en Precoxa. Det følgende Led udvikles til den indre Palpe og første Led af Indergrenen til den ydre Palpe, hvorimod andet Led af Indergrenen bliver til den saakaldte Mellemkæbepalpe. Ydergrenen reduceres Led for Led, til den helt forsvinder og erstattes af den bladformede Dannelse. Endelig dannes et sekundært Skeletstykke, gaaende skraat fra første til andet Led, til Støtte for Lemmets Bevægemuskler.

Bagkæben er noget simplere, men viser dog en Del morsomme Forhold. Stammen er tidligt opdelt i to Led, der her under Udviklingen uddannes til henholdsvis den indre og ydre Palpe; der er altsaa her en Forskel fra første Midtkæbe, hvor disse Lapper dannedes af sidste Led af Stammen og første Led af Indergrenen.

Lemmet har yderligere en enleddet Indergren, der udvikles til den senere Mundfodspalte samt en treleddet Ydergren. Denne sidste synes, ligesom i første Mundfod, at reduceres og erstattes af en bladlignende Dannelse. Endelig fraspalter andet Led i Stammen ret sent i Udviklingen et lateralt Skeletstykke, det saakaldte Precoxa, som alene ved denne Tilblivelse viser sin sekundære Karakter.

Der følger derefter en almindelig slægtskabsmæssig Betragtning, idet det paavises, at Kæberne under Udviklingen omdannes til Typen paa en Bladfod, som vi f. Eks. kender den hos Vandpytternes Vandlopper. Dette tages som et yderligere Bevis for det af Forfatteren tidligere fremsatte Synspunkt (1945, 1947b), at Bladfoden maa opfattes som en Afledning fra Spaltefoden.

Planche I.

Figs. 1—6. Eggs of *Meganyctiphanes norvegica*.

Fig. 1. With outer egg-membrane, in the following figures this membrane has been removed.

Fig. 2. Stage of 16 cells.

Fig. 3. Gastrula.

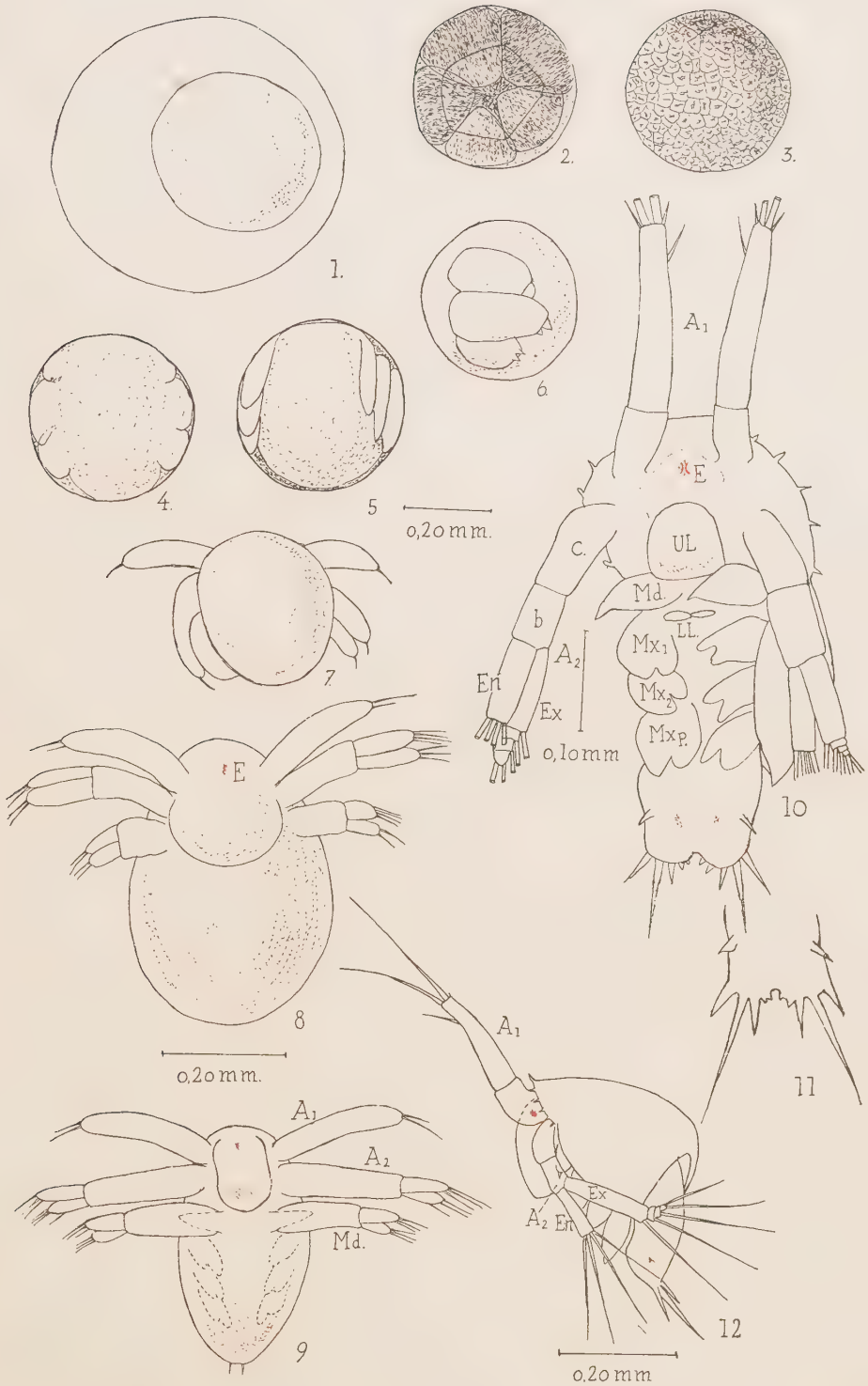
Figs. 4—6. Same egg with incipient formation of the embryo viewed from different sides. The beginning of the three pairs of Nauplius limbs distinctly seen.

Fig. 7. Nauplius before the bursting of the egg-membrane.

Fig. 8. Large Nauplius with incipient formation of eye E. and strongest pigmentation in the abdomen.

Fig. 9. Second Nauplius stage. Shows the distribution of the pigment and the incipient formation of the Metanauplius limbs beneath the skin.

Figs. 10—12. Metanauplius.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C.
b
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0,10 mm
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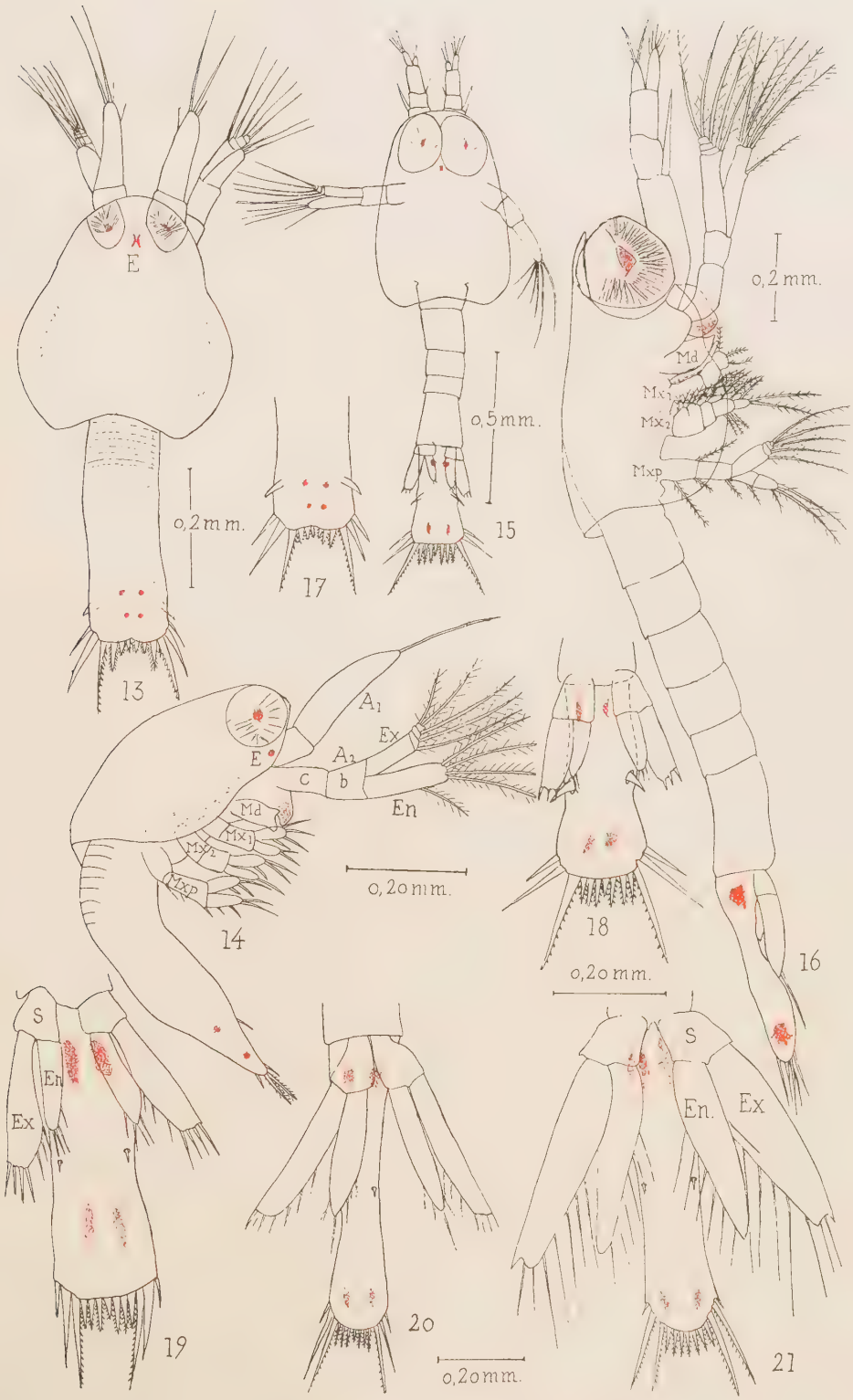
0.20 mm

Planche II.

Fig. 13. 1st Calytopis.
Fig. 14. 2nd Calytopis.
Fig. 15. 3rd Calytopis.
Fig. 16. 1st Furcilia with Pereiopods in developmental stage 1.
Fig. 17. Telson of Calytopis I.
Fig. 18. Telson of Calytopis II.
Fig. 19. Telson of Furcilia I.
Fig. 20. Telson of Furcilia II.
Fig. 21. Telson of Furcilia III.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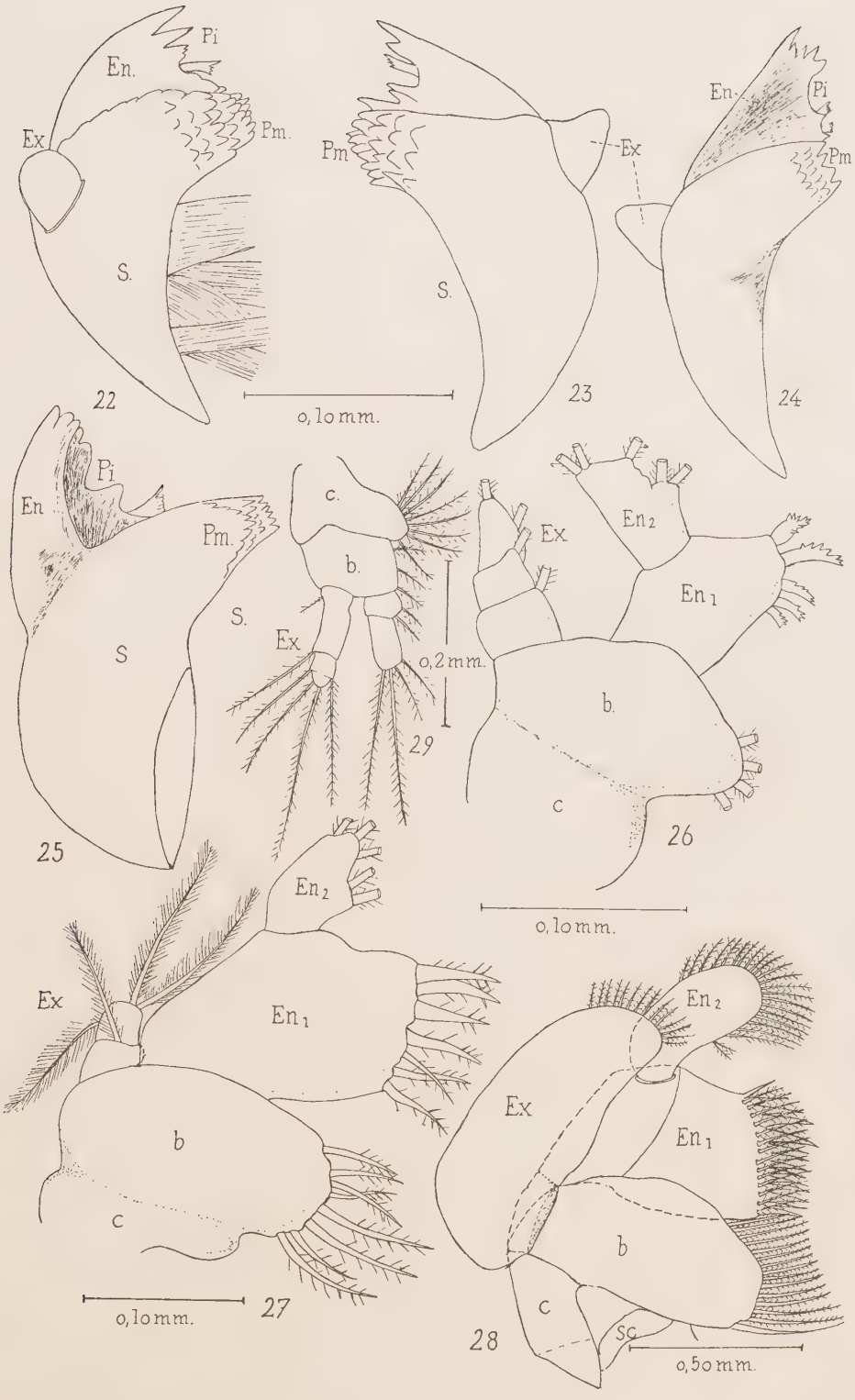
0,20 mm.
14
18
0,20 mm.
S
En
Ex
19
20
0,20 mm.
S
En.
Ex
21

Planche III.

Figs. 22—23. Mandible of Calytopis stage III.
Fig. 24. Mandible of Furcilia I.
Fig. 25. Mandible of Furcilia III.
Fig. 26. First Maxilla of Furcilia I.
Fig. 27. First Maxilla of Furcilia IV.
Fig. 28. First Maxilla of adult specimen.
Fig. 29. Maxilliped of Furcilia I.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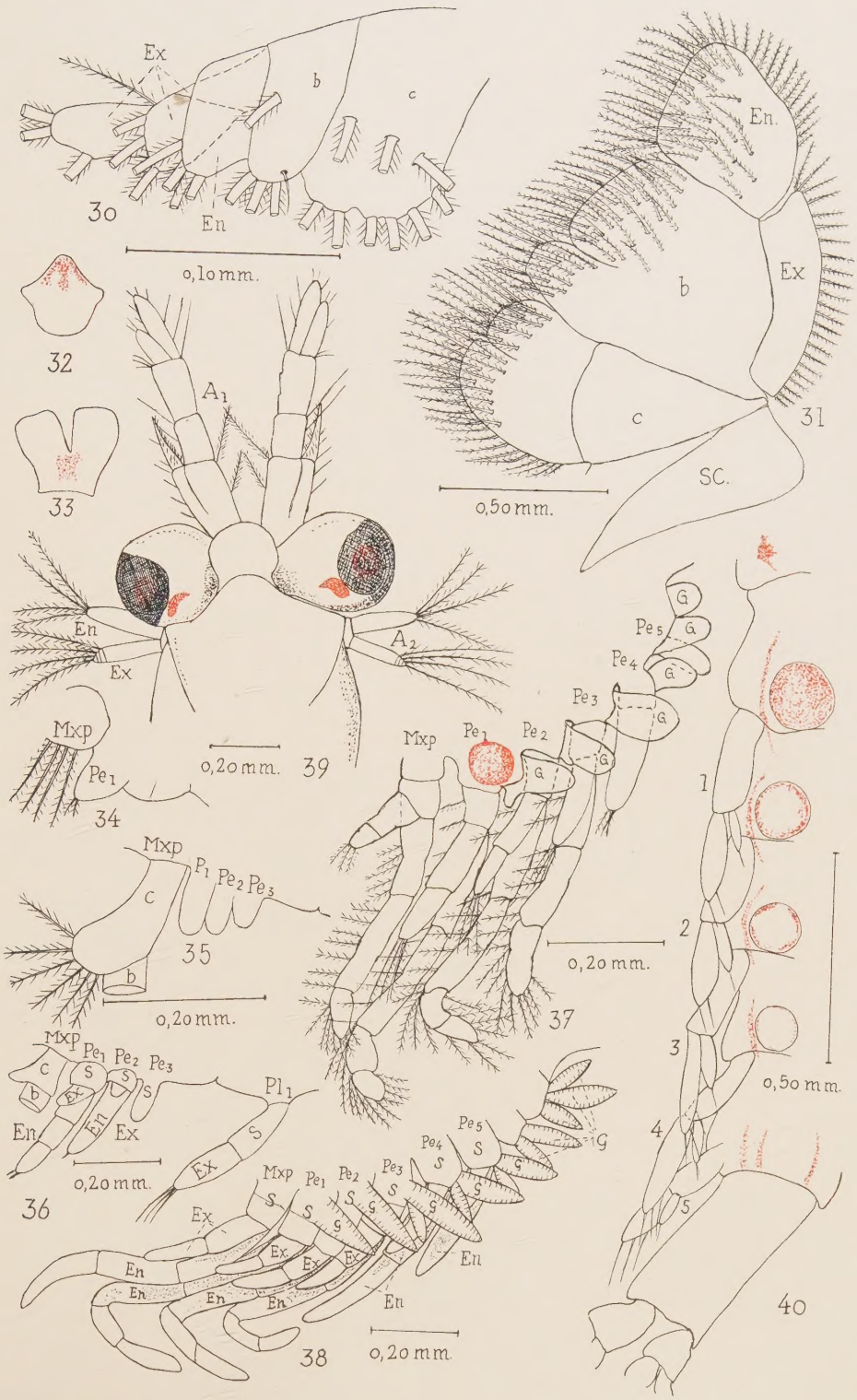
b
c
0,10mm.
27
En2
Ex
En1
b
c
sc
28
0,50mm.

Planche IV.

Fig. 30. Second Maxilla of Furcilia I.
Fig. 31. Second Maxilla of adult specimen.
Fig. 32. Upper lip of Furcilia I.
Fig. 33. Lower lip of Furcilia I.
Fig. 34. Part of Maxilliped and the buds of the successive Pereiopods in developmental stage 2 of Furcilia I.
Fig. 35. Same in developmental stage 3, likewise Furcilia I.
Fig. 36. Part of Maxilliped and succeeding limb-bud in developmental stage 5 of Furcilia II.
Fig. 37. Maxilliped and Pereiopods in Furcilia III in developmental stage 7.
Fig. 38. Maxilliped and Pereiopods in Furcilia IV in developmental stage 9.
Fig. 39. Anterior part of Furcilia III showing a. o. luminescent organ in the eye-stalk.
Fig. 40. Abdomen with pleopods and luminiscent organ of Furcilia IV.


Ex
b
c
En
30
0,10 mm.
32
33
A1
A2
En
Ex
Mxp
Pe1
34
0,20 mm.
39
En.
Ex
b
c
SC.
31
0,50 mm.
Mxp
P1
Pe2
Pe3
c
b
35
0,20 mm.
Mxp
Pe1
Pe2
Pe3
Pe4
Pe5
G
S
Ex
En
Pl1
36
0,20 mm.
Mxp
Pe1
Pe2
Pe3
Pe4
Pe5
S
G
Ex
En
38
0,20 mm.
Mxp
Pe1
Pe2
Pe3
G
37
0,20 mm.
1
2
3
4
5
0,50 mm.
40

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